New Tertiary pycnodonts from the Tilemsi valley, Republic of Mali

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Synopsis

Three new species of *Pycnodus, P. maliensis, P. zeaformis*, and *P. jonesae* are described from the Tertiary deposits of the Tilemsi valley, Republic of Mali. The presence of three other species *P. variabilis, P. munieri* and *P.* cf. *bowerbanki* is noted. The other Tertiary species of *Pycnodus* are redescribed and some synonymies are suggested. It is also suggested that tooth replacement occurs in *Pycnodus* species. Photographs of the holotypes of *Pycnodus pachyrhinus* and *Periodus koenigii* are here published for the first time.

Introduction

The rocks of the Tilemsi valley in northern Mali have long been of interest to geologists. The deposits in the valley range from the Maastrichtian to Middle Eocene. Above this lie terrestrial deposits of post-Eocene age. Several expeditions in the early part of this century recovered a few fossils and these were described by de Lapparent (1905). Furon (1955) described the geological history of north Africa (including the Sahara) but the most detailed work on the area was done by H. Radier who had spent many years studying the Gao region for the Direction des Mines de l'Afrique Occidentale Français. Radier (1959: 322) gives a detailed account of the work done up to 1959 and provides a very extensive bibliography:

Much has been written on the geology and invertebrate palaeontology of the area but there have been very few publications on the vertebrae fossils from the Tilemsi valley. Radier gives a faunal list for each horizon he describes but although he lists pycnodonts, *Ceratodus* sp., *Myliobatis* sp., *Pycnodus variabilis* Stromer, *Phosphichthys thomasi* Arambourg, *Eotrigonodon laevis* Priem, *Trichiurus plicidens* Arambourg, siluroids, *Rhinobatus*, dasyatids and trigonids, there has been very little description of the fish fossils from Mali. Goto (1981) has given a short description of a pycnodont dentition and Lavocat (1955) described dentitions of *Protopterus* sp. from Tamaguélelt.

In 1975 a French expedition to the Tilemsi valley collected many vertebrate fossils. In 1979/80 an Anglo-French expedition, and in 1981 a joint British Museum (Natural History) and Kingston Polytechnic expedition, visited the same area and collected many more vertebrate fossils from the Tertiary rocks, of which the majority were fishes. This paper describes the pycnodont dentitions collected during these three expeditions. Whilst comparing the Mali pycnodonts with other African and European species it became apparent that a revision of Tertiary *Pycnodus* species was needed and this is included in this paper.

The crushing teeth of *Pycnodus* are elliptical and smooth at least in the median rows. In this they differ from the other Tertiary pycnodont genera *Anomoeodus* (with very elongated curved median teeth), *Palaeobalistium* (with subcircular teeth), and *Coelodus* (having median teeth with an apical crenulated indentation). The pycnodont dentitions from Mali are all referred to the genus *Pycnodus* because of the tooth shape.

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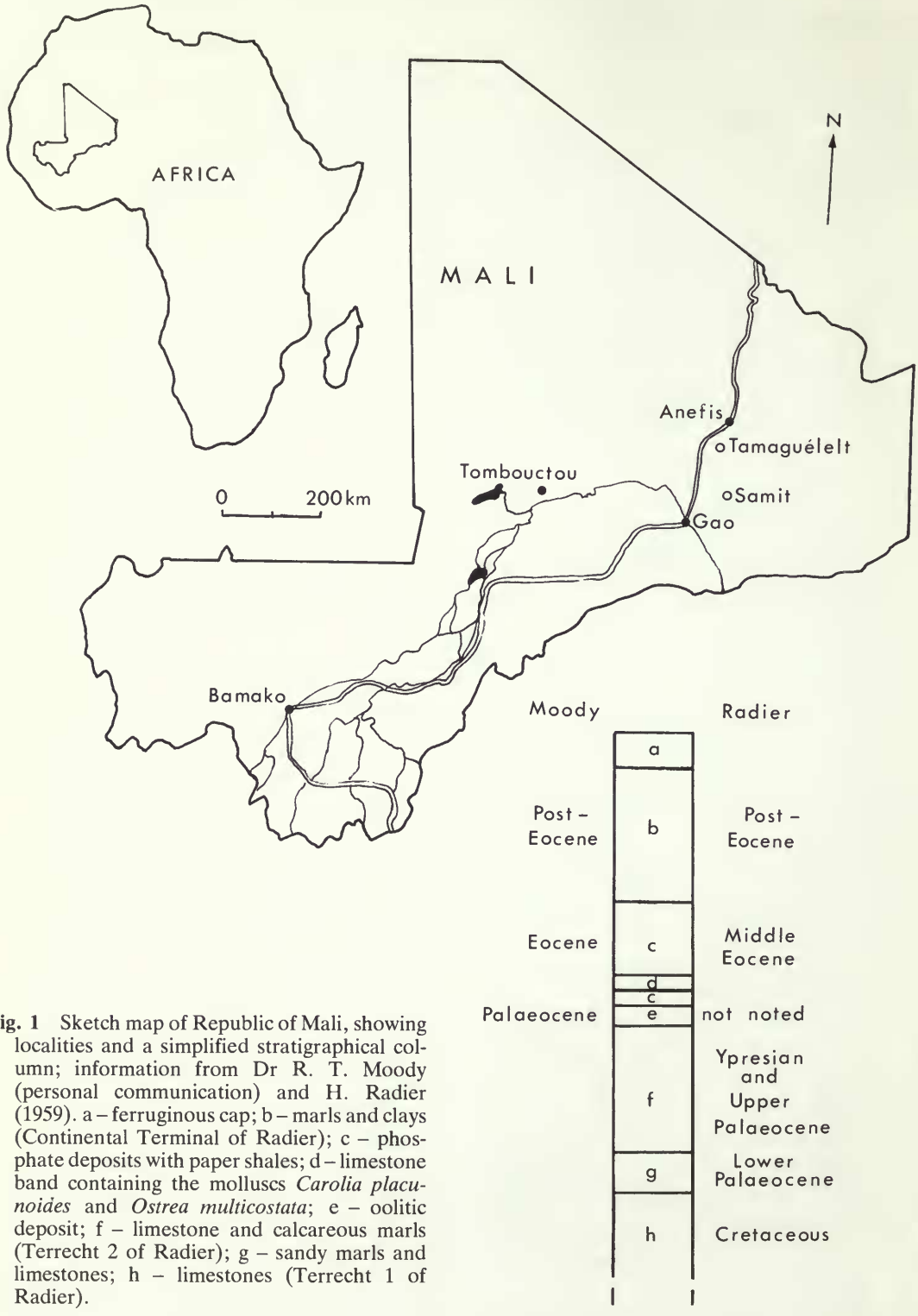


Fig. 1 Sketch map of Republic of Mali, showing localities and a simplified stratigraphical column; information from Dr R. T. Moody (personal communication) and H. Radier (1959). a – ferruginous cap; b – marls and clays (Continental Terminal of Radier); c – phosphate deposits with paper shales; d – limestone band containing the molluscs *Carolia placunoides* and *Ostrea multicostata*; e – oolitic deposit; f – limestone and calcareous marls (Terrecht 2 of Radier); g – sandy marls and limestones; h – limestones (Terrecht 1 of Radier).

Sources of material and methods of study

The pycnodonts reported on here are represented by dentitions (splenials and vomers) only. The associated fish fauna includes many parts of catfish skeletons, *Brychaetus* sp., lungfish dentitions (including *Ceratodus humei* Priem), sparid and centropomid remains, *Myliobatis* sp. and rare sharks teeth. Other vertebrate (*Paleophis* sp., *Dyrosaurus* sp.) and invertebrate remains (molluscs) were also collected.

The pycnodont specimens were collected from two deposits. Most came from the phosphate deposits which have been dated by Radier (1959: 390) as Middle Eocene on the presence of the molluscs *Carolia placunoides* (Cantraine) and *Ostrea multicostata* Deshayes. The molluscs were collected from a limestone band occurring within the paper shales at the bottom of the phosphates. The vertebrate remains come from the phosphates themselves. Similar phosphate beds occur in many parts of north Africa but are usually considered to be at least as old as Ypresian elsewhere in Africa (R. T. Moody, personal communication).

A few pycnodont dentitions were collected from a coarse-grained deposit containing many very small ferruginous ooliths (0·75 mm in diameter). This deposit occurs underneath the lowest paper shale layer of the phosphate deposits. The fish fauna from the oolitic layer is similar to that of the phosphates except that, at the moment, *Ginglymostoma* cf. *angolense* Dartevelle & Casier, several unidentified teleosts, and the new *Pycnodus* cf. *bowerbanki* specimens are restricted to the oolitic deposit, whilst *Ceratodus humei* has only been found in the phosphates. The oolitic deposit was not recorded or described by Radier and no microfossils have yet been found to date it with precision. The deposit lies some way above the limestone from which Apostolescu (1961) described the ostracods *Uroleberis glabella* Apostolescu and *Ambocythere tatteuliensis* Apostolescu. These range throughout the Palaeocene. The oolitic deposit therefore cannot be older than Palaeocene or younger than Middle or Lower Eocene, depending on the age of the phosphate deposit. Madden *et al.* (1979) describe a deposit (the Umm Himar Formation) from the Harrat Hadan area of Saudi Arabia. Just below the fossiliferous horizon, but still in the Umm Himar Formation, in Saudi Arabia there is a deposit with small ferruginous ooliths and a root/burrow system very similar to that found in Mali. The fauna of the Umm Himar Formation is very similar to that from the oolitic deposit in Mali. Madden *et al.* (1979) date the Umm Himar Formation as Upper Palaeocene based on the first and last appearances of various elements in their fauna. They record *Ginglymostoma blanckenhorni* Stromer, *Ginglymostoma maghrebianum* Casier and catfish, all with a first appearance in the Palaeocene, and *Ceratodus humei* which has a last appearance in the Palaeocene (Tabaste 1963). In Mali *Ginglymostoma* cf. *angolense* (an Ypresian species) and catfish were found in the oolitic deposit. However, two specimens of *Ceratodus humei* were found in the overlying phosphates which contain molluscs thought to be Middle Eocene by Radier (1959: 378). This would be the youngest appearance of *Ceratodus humei* and casts doubt on the evidence of Madden *et al.* (1979) for a Palaeocene age of the Umm Himar Formation as based on the last appearance of *C. humei.*

The pycnodonts described herein were collected from two main localities, the first at Tamaguélelt about 25 km NNE of In Tasit, in the Gao region at 0° 15′ E, 17° 36′ N. Both the phosphates and the oolitic deposit occur around the Tamaguélelt outlier. The second site is about 30 km north-east of Samit wells at 1° 00′ E, 16° 50′ N, where only the oolitic deposit was explored. Fig. 1 shows the localities mentioned and a simplified stratigraphical column. The specimens are now in the collections of the British Museum (Natural History) (those numbered BMNH with or without a 'P' prefix) and in the Laboratoire de Paléontologie, Université de Pierre et Marie Curie, Paris (those with prefixes MLM and TGE). One specimen collected by Lavocat from an unknown locality in the Gao region is also included in the descriptions. This specimen is from the collections of the Laboratoire de Paléontologie de l'Université des Sciences et Techniques du Languedoc, Montpellier. Eighty-seven specimens were measured for the present study, of which 52 are splenials and 35 are vomers. The specimens are very well preserved and all those used in the following descriptions show more than one tooth row, and some of the specimens are almost complete. This is not usual in the study of Tertiary pycnodont

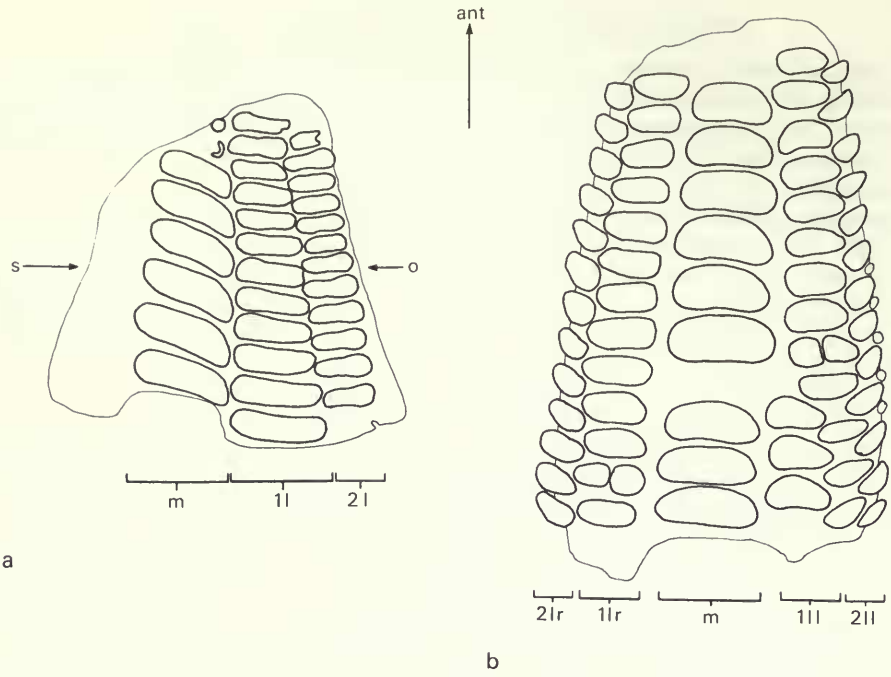


Fig. 2 Outline drawings of splenial and vomer to show terminology used; ant – anterior. a, splenial (lower dentition) of *P. maliensis* sp. nov.; m – medial row; 1l – first lateral row; 2l – second lateral row; s – symphyseal edge; o – outer edge. b, vomer (upper dentition) of *P. zeaformis* sp. nov.; m – median row; 1ll – first lateral row left; 2ll – second lateral row left; 1lr – first lateral row right; 2lr – second lateral row right. Directions refer to in-life position.

dentitions and allows very complete measurements and comparisons of the tooth rows on a large sample. It also allows some idea to be gained of the variation within a species. Most previous descriptions of species erected only on dentitions have been based on only one or two specimens, and those often very incomplete.

In the descriptions of the species in this paper the following terminology is used (Fig. 2). The tooth rows in the splenial are named medial for the innermost main row, first lateral for the next outer row, second lateral for the next outer and so on to the outermost row. Most of the specimens in the sample have only first and second lateral rows, but a few have more. In the vomer the tooth rows are named median for the row in the centre line, then first lateral (right and left) for the next outer rows on either side of the median row, then second lateral (right and left) and so on to the outermost rows. The individual teeth were measured such that length refers to the greatest anteroposterior measurement, and breadth (or width) refers to the greatest transverse measurement. The terms longer and shorter are relative to the first measurement, and the terms broader, wider and narrower are relative to the second. The length as a percentage of the breadth of each tooth has been measured and the average for each row calculated and used in the descriptions and tables as a character for comparing the species. Tooth shape in each row is another main character used to distinguish species.

Pycnodus dentitions usually have three main rows on the splenials and five on the vomers. However, this character is variable as is shown by the Mali specimens and extra rows may occur. In some cases this may be a growth phenomenon and what is normally a single row of elliptical teeth is instead represented by a double row of smaller teeth. Quite often in *Pycnodus* dentitions two small teeth occur where one would expect only one tooth in the main rows. It is also common to find that in the anterior region of the splenials and vomers the dental pavement is formed by

many small and round, irregularly-arranged teeth. This indicates that *Pycnodus* dentitions can show quite a variation of tooth shape and it is only with great doubt that isolated pycnodont teeth can be identified. In the Mali fauna there are enough complete dentitions to see that, in general, three splenial and five vomerine tooth rows are present, whose teeth show fairly constant characters which can be used for identification purposes. In isolated specimens from other localities determinations can be positive only when at least three tooth rows are represented in one specimen.

The fauna from Mali contains two species based on splenials and four species based on vomers. Three of these species are new, the others being *P. variabilis* Stromer, *P. munieri* Priem, and *P.* cf. *bowerbanki* Egerton. It is likely that species erected only on splenials may be conspecific with those associated species erected on vomers, but in the Mali fauna there are no criteria for determining which if any of the splenial and vomerine species are conspecific since all the species occur at the one locality. Egerton (1877) suggested that upper and lower jaws tend to have similarly-shaped teeth and this would indicate that two of the new Mali species are the same, especially since they are of the same general size range. However, study of associated dentitions found in complete specimens in other pycnodonts does not seem to uphold this (R. Nursall, personal communication). The two species are therefore given different names.

Descriptions of new species

Infraclass **ACTINOPTERI** Cope, 1871

Series **NEOPTERYGII** Regan, 1923

Order **PYCNODONTIFORMES** Berg, 1940

Family **PYCNODONTIDAE** Agassiz, 1832

Genus ***PYCNODUS*** Agassiz, 1833

Pycnodus maliensis sp. nov.
Figs 2a, 3–8

Diagnosis. Splenial dentitions with medial and first lateral teeth on average almost three times as wide as long; second lateral teeth on average slightly more than twice as wide as long; the outer ends of the medial teeth are turned posteriorly thus giving a bevelled appearance; medial teeth only 25% wider than the first lateral teeth.

Name. After the country in which it is found.

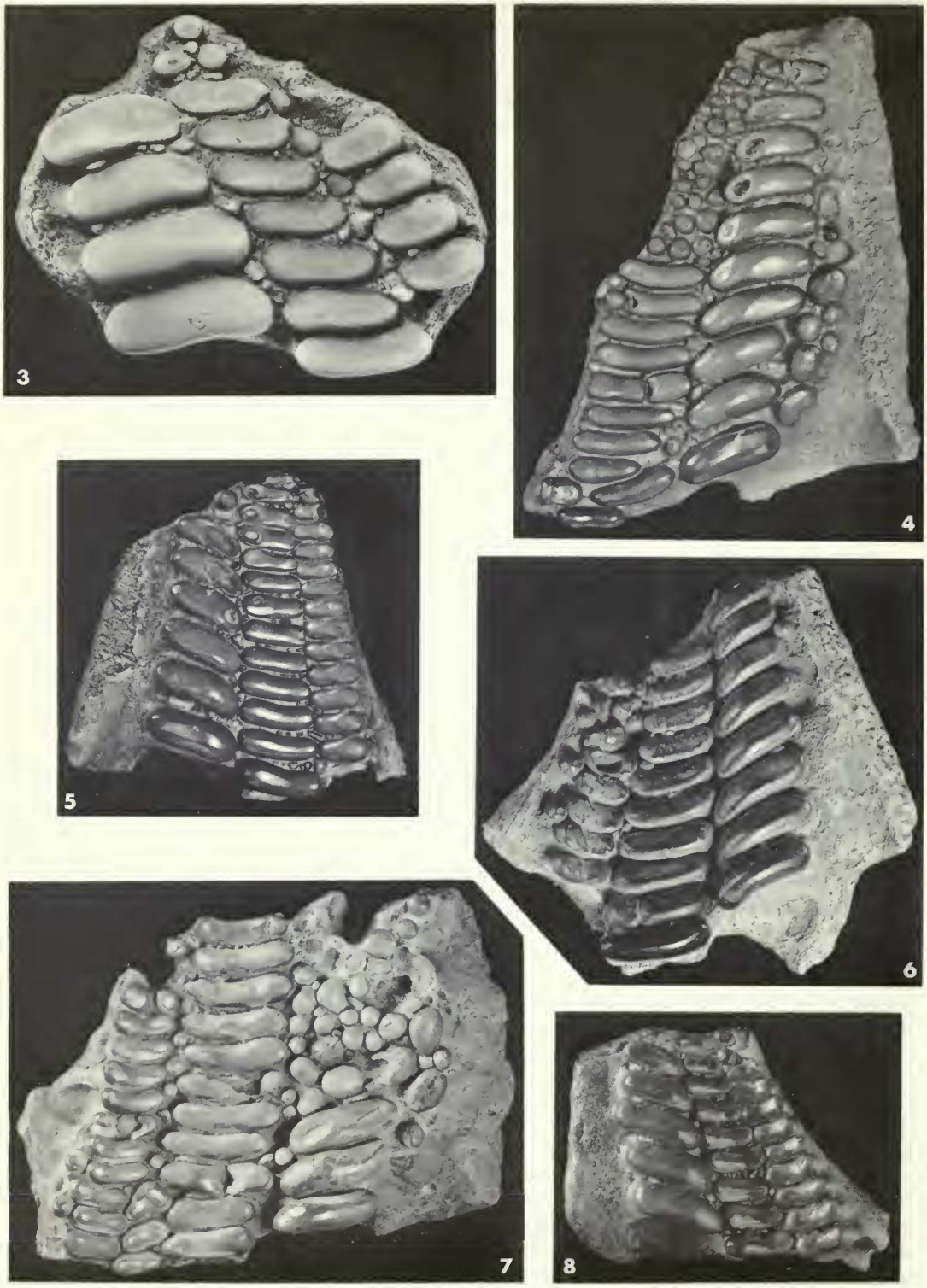
Holotype. BMNH P.61048, phosphate deposit, ? Middle Eocene. Tamaguélelt, Republic of Mali.

Paratypes. TGE 601–18, MLM 1–15, BMNH P.60624–34, P.60919–20 (46 specimens).

Other material. Fifty-six other specimens collected in 1981, and now in the collections of the British Museum (Natural History), are also identified as this species.

Horizons and localities. The holotype, paratypes and 49 of the other specimens were collected from the phosphate deposit at Tamaguélelt. Seven specimens were collected from the oolitic deposit at Tamaguélelt.

Description. The species is based on splenial dentitions only. The splenials are medium-sized compared with other *Pycnodus* species and the medial teeth of the type material average 12·8 mm in width. The medial teeth are more or less elliptical in shape but with a slightly convex anterior border and a slightly concave posterior border, especially towards the outer ends where the ends of the teeth turn posteriorly. The medial row usually has the largest teeth in which the width averages three times the length. The teeth in the first lateral row are also very wide compared to their length, the ratio being 3:1 again. The first lateral teeth are elliptical but the anterior border is slightly concave and the posterior one slightly convex. The teeth in the first



Figs 3–8 Splenials of *P. maliensis* sp.nov., all except Fig. 3 ×1. Fig. 3, **holotype** BMNH P.61048, ×2. Fig. 4, paratype BMNH P.60631. Fig. 5, paratype BMNH P.60625. Fig. 6, paratype TGE 601. Fig. 7, paratype BMNH P.60628. Fig. 8, paratype BMNH P.60920.

lateral row are on average 9·9 mm wide. The teeth in the second lateral row are narrower, twice as wide as long and are also elliptical in shape with more or less parallel anterior and posterior borders. Small circular teeth commonly occur between the tooth rows and also in the anterior region of many of the splenials. The tooth-bearing surface of the splenial has a sinusoidal profile when viewed from behind. This is a character common to all *Pycnodus* species.

Pycnodus zeaformis sp. nov.
Figs 2b, 9–14

1981 'Pycnodont' Goto: ii–2; fig. 3; pl. 1.

Diagnosis. Vomerine dentitions with median teeth on average 2·5 times as wide as long; first lateral teeth slightly more than twice as wide as long; second lateral teeth almost twice as wide as long; longest axes of teeth in lateral rows parallel to those of median teeth.

Name. After the plant *Zea* because of the resemblance of the vomers to corn cobs.

Holotype. BMNH P.61049, phosphate deposit, ? Middle Eocene. Tamaguélelt, Republic of Mali.

Paratypes. TGE 619–20, 622, 624, MLM 16–19, BMNH P.60640–3, P.60915, P.60921 (14 specimens).

Other material. Eight other specimens collected in 1981, and now in the collections of the British Museum (Natural History), are also identified as this species.

Horizons and localities. The holotype, paratypes and seven other specimens were collected from the phosphate deposits at Tamaguélelt. One specimen was collected from the oolitic deposit at Tamaguélelt.

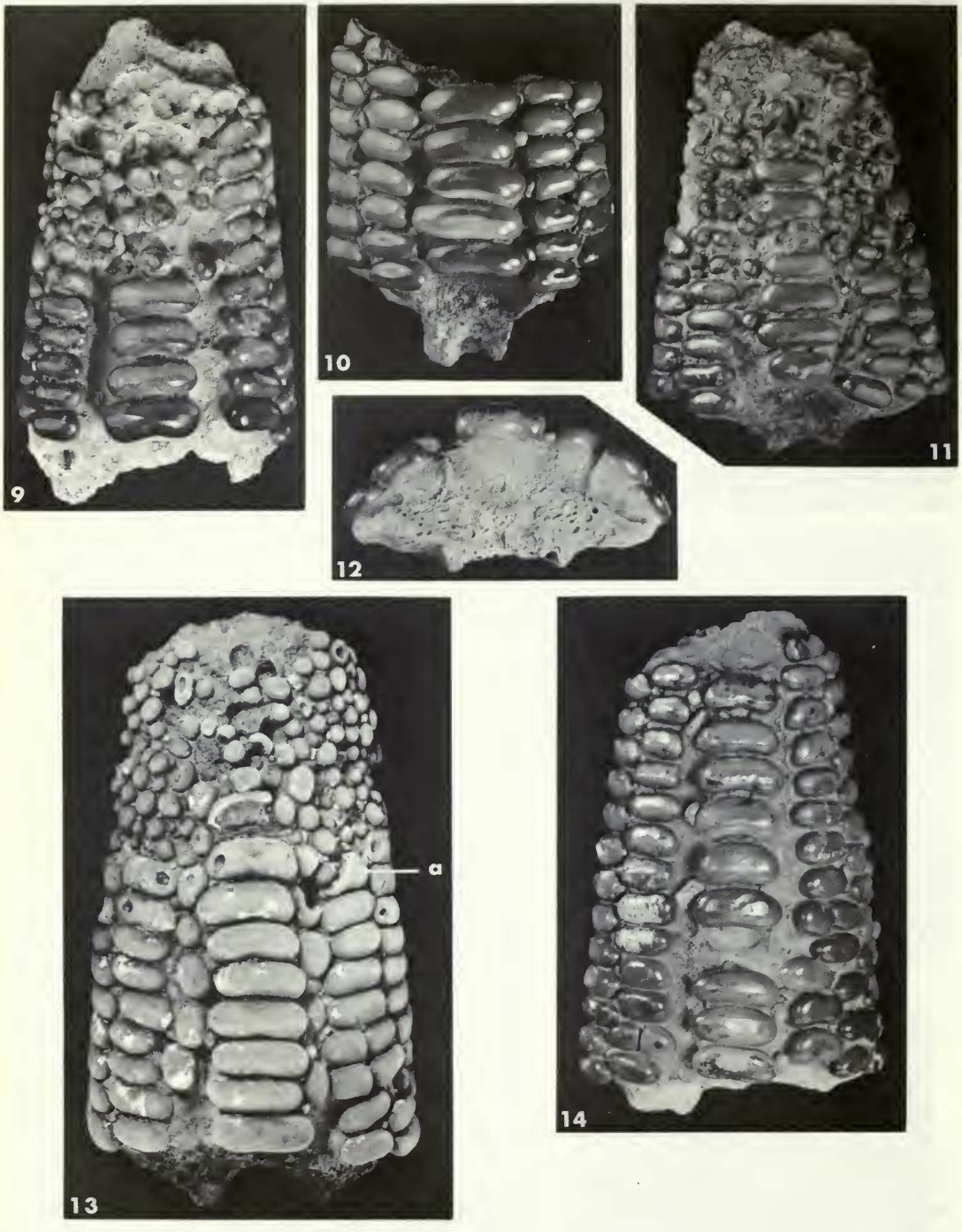
Description. The species is known by vomers only and these are medium-sized compared to those of other *Pycnodus* species. The width of the median teeth is 11 mm on average. The median row has the largest teeth and these are bean-shaped with a convex anterior border. The median teeth are about 2·5 times as wide as long. The first lateral teeth are subrectangular in shape and just over twice as wide as long, a feature not found in vomers of any other *Pycnodus* species. The first lateral teeth have their longest axes parallel to those of the median teeth. The teeth of the first lateral rows are shorter than those of the median row so that there are more lateral teeth per unit length. This means that some of the first lateral teeth are aligned with median teeth and some alternate with them. The teeth in the second lateral rows tend to alternate with those in the first lateral rows since they are about the same length. The second lateral teeth are ovoid or subrectangular and almost twice as wide as long. The longest axes in these are also parallel to those of the first lateral and median teeth, a character not present on the vomers of any other *Pycnodus* species. The teeth in the third and fourth lateral rows, where present, are ovoid and narrower than those of the second lateral rows. They have their longest axes parallel or at a slight angle to those of the other rows. The tooth-bearing surface of the vomer forms an arch when viewed from behind (Fig. 12), a character common in *Pycnodus* species.

Pycnodus jonesae sp. nov.
Figs 15–17, 26b

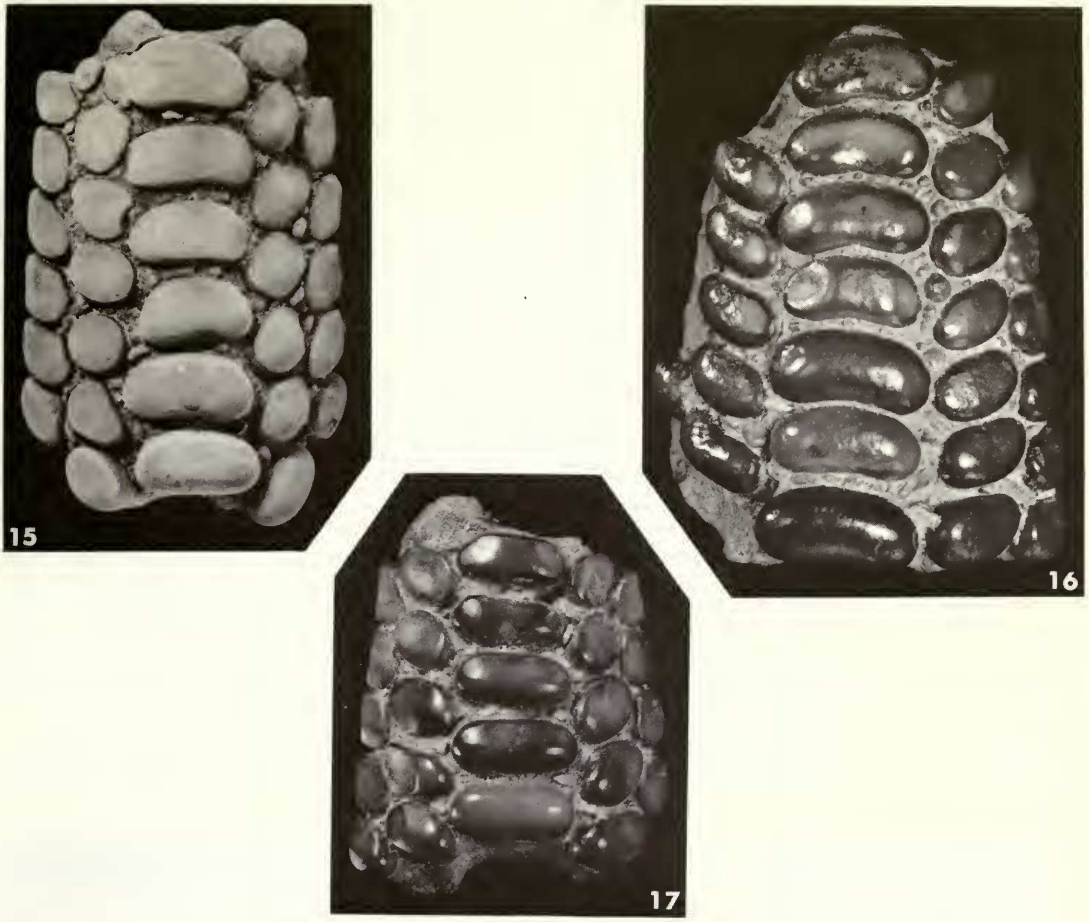
Diagnosis. Vomerine dentitions with elliptical or bean-shaped median teeth almost 2·5 times as wide as long; first lateral teeth just over 1·5 times as wide as long, with longest axes orientated at about 30° to those of median teeth; second lateral teeth only just wider than long and orientated at about 60° to median teeth.

Name. In memory of Miss M. Jones who died on the 1979/80 expedition to Mali.

Holotype. BMNH P.61050, phosphate deposit, ? Middle Eocene. Tamaguélelt, Republic of Mali.



Figs 9–14 Vomers of *P. zeaformis* sp. nov., all ×1. Fig. 9, paratype TGE 620. Fig. 10, **holotype** BMNH P.61049. Fig. 11, paratype BMNH P.60921. Fig. 12, paratype BMNH P.60643, viewed from behind. Fig. 13, paratype BMNH P.60915 (*a* see text, p. 24). Fig. 14, paratype BMNH P.60643.



Figs 15–17 Vomers of *P. jonesae* sp. nov., all ×2. Fig. 15, paratype BMNH P.60636. Fig. 16, **holotype** BMNH P.61050. Fig. 17, paratype TGE 623.

PARATYPES. TGE 623, MLM 20, 21, BMNH P.60636–7 (5 specimens).

OTHER MATERIAL. Five other specimens collected in 1981, and now in the collections of the British Museum (Natural History), are also identified as this species.

HORIZONS AND LOCALITIES. The holotype, paratypes and four other specimens were collected from the phosphate deposit at Tamaguélelt. One specimen was collected from the oolitic deposit at Tamaguélelt.

DESCRIPTION. The species is known by vomerine dentitions only. These are on average slightly smaller than those of *Pycnodus zeaformis*, and have median teeth averaging 9·1 mm in width. The median teeth are elliptical or bean-shaped and almost 2·5 times as wide as long. This species differs from *P. zeaformis* in having oval first lateral teeth which have their longest axes orientated at about 30° to those of the median teeth. The first lateral teeth are just over 1·5 times as wide as long. The teeth of the second lateral rows are oval and marginally wider than long. Oval first and second lateral teeth are common in Tertiary *Pycnodus* species but *P. jonesae* differs from these in the shape of the median teeth and their greater relative width. The only other *Pycnodus* species with median teeth of the vomers 2·5 times as wide as long are *P. zeaformis*, which does not have oval lateral teeth, and *P. savini* Priem, which is much larger

and has different-shaped median teeth (Fig. 26a). The tooth-bearing surface of *P. jonesae* forms an arch when viewed from behind.

Revision of the Tertiary species of *Pycnodus*

As stated in the Introduction many Tertiary species of *Pycnodus* have been erected on the basis of isolated vomerine and splenial dentitions, of varying completeness. Study of the great number of Mali pycnodont specimens, showing large parts of the dentition, has enabled me to appreciate the range of variability to be expected within any one species. On examining the figures and, in some cases, the material of other Tertiary species of *Pycnodus* I believe that some of them may simply be variants of one another. I will therefore suggest some synonymy. In a few

Table 1 Relative measurements[1] of the teeth of splenials of Tertiary *Pycnodus* species. (A) Length as a percentage of width of teeth, average of each tooth row with ranges given in brackets and number of specimens measured. (B) Average width of teeth in mm, all teeth in each row measured. (C) Average width of first lateral teeth as a percentage of average width of medial teeth.

	A				B		
	medial	first lateral	second lateral	number of specimens measured	medial	first lateral	C
P. maliensis	37·2 (29–46)	35·4 (25–47)	48·1 (33–61)	47	12·8	9·9	77·2
P. praecursor Cappetta's specimen	43·8	42·2	57·5	1	14	9·0	64·2
P. toliapicus + *P. koenigi*	46·6 (40–52)	68·9 (63–76)	80·3 (75–87)	6	15·0	8·6	57·3
Stromer's specimens of *P. variabilis* excluding St2	49·9 (45–58)	58·8 (53–70)	78·1 (65–100)	6	14	9·3	66
P. variabilis var. *togoensis*	51·1 (46–56)	56·0 (54–58)	77·9 (70–86)	3	11	7·4	67·2
P. praecursor D & C specimen	49·1	52·7	69·6	1	9·1	6·8	74·7
P. vasseuri	55·1	55·4	75	1	12	7·7	64·1
P. pellei	43·1	61·9	56·0	1	22	10·5	47·7
P. mokattamensis	56·2	80·5	53·8	2	20	11	55
Specimen St2	44·2	46·6	75·5	1	8	6·5	81·2
BMNH P.18823	42·6	42·3	—	1	7·2	5·3	73·6
P. bowerbanki	40·4	47·1	72·4	1	25·5	16·3	63·9
GAO 7	38·1	47·2	74·2	1	21·4	13·0	60·7
BMNH P.60917	48·2	45·3	75·3	1	21·7	13·1	60·3
Madden's large *Pycnodus* sp.	37·8	50	—	3 teeth only	31·6	—	—

[1] A copy of the full measurements of the type material of *P. maliensis* is deposited in the Palaeontology Library of the British Museum (Natural History).

instances vomerine and splenial dentitions have been assigned to the same species, usually because they have been found in the same deposits. However, as we can only be certain of association of vomers and splenials in intact heads of pycnodonts I will treat splenial and vomerine material separately.

Splenials.
Table 1 is a comparison of the length as a percentage of the breadth of splenial teeth in Tertiary *Pycnodus* species.

Pycnodus toliapicus Agassiz
Figs 18–20

1839–44 *Pycnodus toliapicus* Agassiz: 196; pl. 72a, fig. 55. Ypresian, England.
1839–44 *Periodus koenigii* Agassiz: 201; pl. 72a, figs 61, 62 (misprinted in caption as figs 60, 61). Ypresian, England.
1850 *Periodus koenigii* Agassiz; Dixon: 205; pl. 10, fig. 13. Bracklesham beds, England.
1877 *Pycnodus toliapicus* Agassiz; Egerton: 53. Ypresian, England.
1895 *Pycnodus toliapicus* Agassiz; Woodward: 277. Ypresian, England.
1895 *Pycnodus koenigi* (Agassiz) Woodward: 278. Bracklesham beds, England; Middle Eocene, Belgium.
1905 *Pycnodus variabilis* Stromer: 101; pl. 16, figs 35, 37, *not* fig. 36. Middle Eocene, Egypt.
1910 *Pycnodus variabilis* var. *togoensis* Stromer: 485; figs 14a, b; textfig. 2. Landenian, Togo.
1920 *Pycnodus toliapicus* Agassiz; Bell: 12; pl. 11, fig. 16.
1935 *Pycnodus variabilis* var. *togoensis* Stromer; White: 40; fig. 9, *not* fig. 8. Landenian, Nigeria.
1950 *Pycnodus toliapicus* Agassiz; Casier: 23; pl. 2, fig. 6. Lutetian, Belgium.
1966 *Pycnodus toliapicus* Agassiz; Casier: 104; pl. 11, figs 4a–b. Ypresian, England.

The holotype of *Pycnodus toliapicus* is an incomplete specimen. At the same time Agassiz described *Periodus koenigii* based on a single worn splenial (BMNH P.3759). In 1877, whilst

Figs 18–20 Splenials of *P. toliapicus*, all ×1. Fig. 18, BMNH 38825. Fig. 19, BMNH 25697. Fig. 20, BMNH P.3759 (holotype of *Periodus koenigii*).

describing more specimens (BMNH 38825–6, Fig. 18) of *P. toliapicus*, Egerton suggested that *P. toliapicus* and *P. koenigi* were synonymous. After restudy of the holotypes and other specimens I agree with this suggestion. Woodward (1895: 278), in describing the two species, also says that they are usually considered to be synonymous. He erroneously cites the holotype of *P. koenigi* as BMNH 25697 (Fig. 19) from the Bracklesham beds, Sussex, Dixon collection. The specimen of *P. koenigi* figured by Agassiz is in fact BMNH P.3759 (Fig. 20) from the London Clay, Sheppey, Kent, from the Enniskillen collection. Woodward describes P.3759 as 'a small abraded specimen' of *P. toliapicus*, thus showing that he could not easily distinguish between *toliapicus* and *koenigi*. BMNH 25697 is the specimen figured by Dixon (1850), although Woodward does not mention this. Splenials of *P. toliapicus* differ from those of *P. maliensis* in all characters mentioned in the diagnosis (p. 5).

At this point I will discuss specimens referred to two named taxa, *Pycnodus variabilis* Stromer and *Pycnodus variabilis* var. *togoensis* Stromer (Figs 21a, c, d, h, i). Stromer (1905: 101) erected *P. variabilis* for specimens from the lowest Middle Eocene of Mokattam, Egypt. Stromer's splenials St5 and M1 (1905: pl. 16, figs 35, 37, St5 redrawn here as Fig. 21a) do not appear to differ significantly from the holotypes of *toliapicus* or *koenigi*. In fact Stromer recognized the similarity and stated that the specimen described by Dixon (1850) as *P. koenigi* is the same as his specimens and should be synonymized with them. Stromer, however, believed that his specimens and Dixon's specimen were different from *toliapicus* and *koenigi*. As stated above neither Woodward nor I regard Dixon's specimen as representing a species different from *koenigi* (Woodward even thought it was the holotype), or from *toliapicus*, and therefore the splenials St5 and M1 figured by Stromer should be assigned to the species *toliapicus*.

Another of Stromer's splenial specimens (St2; Stromer 1905: pl. 16, fig. 36, redrawn here as Fig. 21h) differs from the splenials St5 and M1 in that the medial and first lateral teeth are relatively wider in St2. The tooth proportions are also smaller (average width of medial teeth 8 mm) than the other splenials (average width of medial teeth 14 mm) figured by Stromer. Stromer noted the differences in his specimens (hence the name *variabilis*) but did not think they warranted different species. I, however, believe that the differences are significant enough for St2 to be regarded as a different species from the other splenials, since in the proportions of the medial and first lateral teeth St2 differs from the other *variabilis* splenials as much as Stromer's specimens St5 and M1 differ from *P. maliensis* splenials. St2 resembles *P. maliensis* in the proportions of the medial and first lateral teeth (which fall just within the upper limit of *maliensis*). However, the second lateral teeth are subcircular in St2 and very different from those in *maliensis*. Because of the relatively wide medial and first lateral teeth St2 differs from other Tertiary *Pycnodus* species, and therefore remains identified as *P. variabilis* (p. 17). The other splenials described by Stromer (1905: 191) as *P. variabilis* but not figured appear, from the measurements and descriptions given, to be similar to St5 and M1, but without examination of the specimens I cannot be definite about their identification.

Stromer (1910: 485; figs 14a, b, fig. 2) described *Pycnodus variabilis* var. *togoensis* on splenials, from the Landenian (Leriche 1913) of Adabion, Togo. White (1935: 40; fig. 9) refers a similar specimen from the Landenian of Sokoto, Nigeria to this variety also. I can see no difference between this variety and Stromer's St5 and M1. The medial teeth are supposed to be relatively wider in var. *togoensis*, but the difference is very slight except in the much larger specimen shown by Stromer (1910: fig. 2) which is in fact very similar to Egerton's specimens of *P. toliapicus*, BMNH 38825–6 (Fig. 18). The specimen figured by White (1935: fig. 9, BMNH P.18824, redrawn as Fig. 21c) has medial teeth of the same proportions as those of St5 and M1. White's reason for identifying his specimens as *P. variabilis* var. *togoensis* rather than *P. variabilis* was their association with large individual teeth of similar proportions to the large specimen figured by Stromer (1910: fig. 2) as *P. variabilis* var. *togoensis*. Because of their similarity to St5 and M1 the specimens identified by Stromer as *P. variabilis* var. *togoensis* and BMNH P.18824 should be assigned to *P. toliapicus*.

BMNH P.18823, a splenial from the Landenian of Gada, Nigeria, described by White (1935: 40; fig. 8, redrawn here as Fig. 21i) as *P. variabilis* var. *togoensis* differs from both BMNH P.18824 and Stromer's examples of *P. variabilis* var. *togoensis* in having relatively wider medial

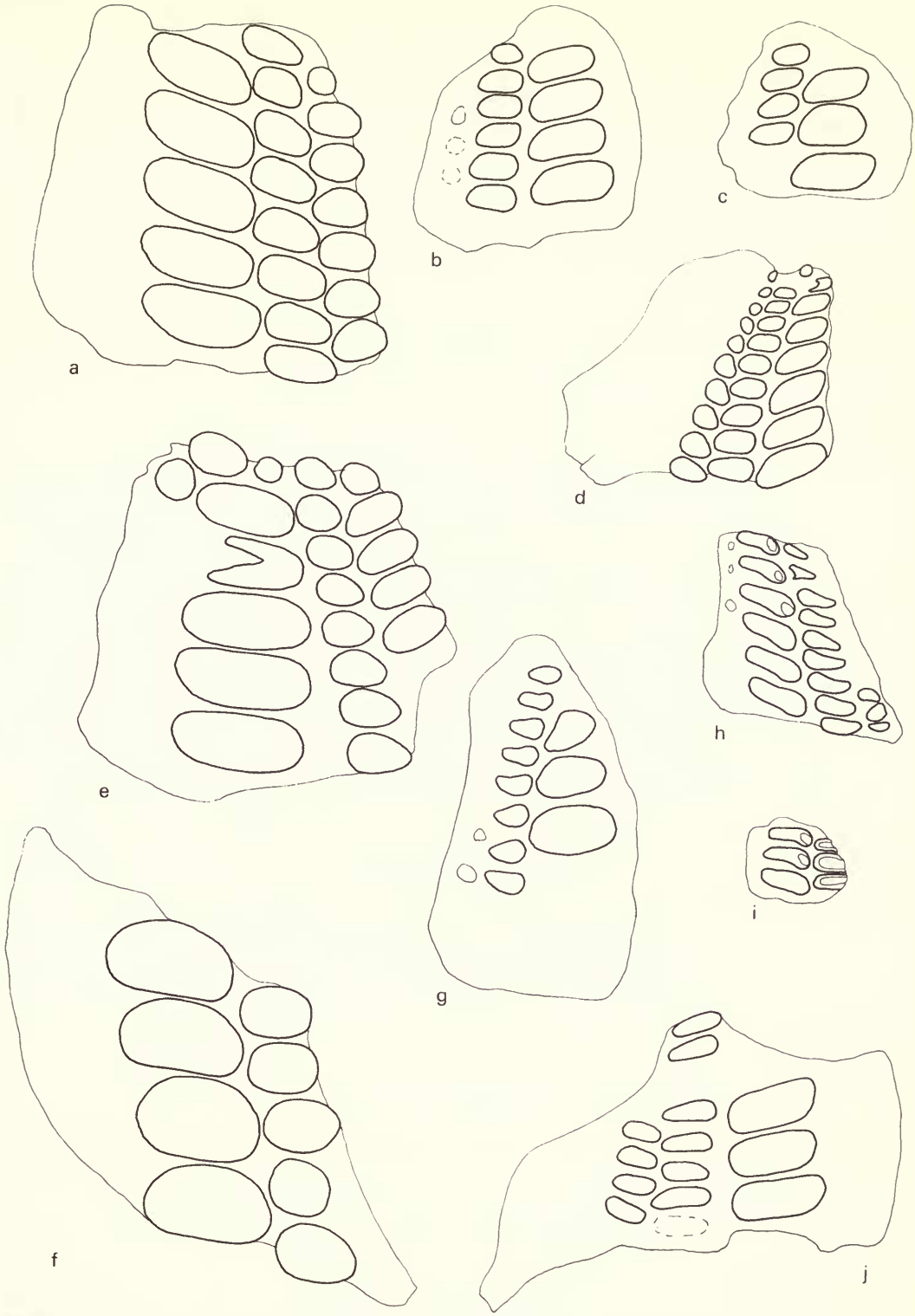


Fig. 21 Outline drawings of splenials of *Pycnodus* species to show differences in tooth shapes. All ×1, drawn from original photographs or drawings. a, *P. variabilis*, St5. b, *P. praecursor*. c, *P. variabilis* var. *togoensis*, BMNH P.18824. d, *P. variabilis* var. *togoensis*. e, *P. pellei*, holotype. f, *P. mokattamensis*. g, *P. vasseuri*, holotype. h, *P. variabilis*, St2. i, *P. variabilis* var. *togoensis*, BMNH P.18823. j, *P.* cf. *praecursor*.

and first lateral teeth. In these respects it resembles Stromer's (1905) St2, as White himself points out (1935: 42). Like St2 the proportions of the medial and first lateral teeth of BMNH P.18823 fall within the range of those of *P. maliensis*, but because of the lack of second lateral teeth it is not possible to say whether P.18823 is an example of *P. maliensis* or the same as St2. The teeth of BMNH P.18823 and St2 are similar in size and smaller than most specimens of *P. maliensis*; it is therefore probable that BMNH P.18823 is the same species as St2, that is *P. variabilis* as restricted here.

Pycnodus praecursor Dartevelle & Casier
Fig. 21b

1943 *Pycnodus variabilis* Stromer; Dartevelle & Casier: 90, name only.
1949 *Pycnodus praecursor* Dartevelle & Casier: 212; pl. 17, figs 1, 3 (?4, 5). Palaeocene (Montian), Landana, Angola.

This species differs from *P. maliensis* in all characters listed on p. 5. It is not significantly different from *P. toliapicus*. Dartevelle & Casier suggested that *praecursor* is similar to *variabilis* (as defined by Stromer) but ancestral to it because of its earlier occurrence. The splenials of *praecursor* are similar to Stromer's St5 and M1 and I believe that they should be reassigned to *P. toliapicus* also.

Cappetta (1972: 222; pl. 11, figs 3, 4) described two splenials from the Palaeocene of Niger as *Pycnodus* cf. *praecursor*. However, one specimen (1972: pl. 11, fig. 3, redrawn here as Fig. 21j) differs from those described by Dartevelle & Casier in having relatively wider medial, first lateral and second lateral teeth. The proportions of these teeth fall within the range of those of *P. maliensis*, but this specimen does not have the bevelled medial teeth characteristic of *maliensis*. The other specimen figured by Cappetta (pl. 11, fig. 4) has medial teeth only but the proportions of these fall within the range of those of *maliensis*. Without the first and second lateral teeth it is not possible to confirm whether this specimen is *maliensis* or, for example, *P. pellei* which also has medial teeth of similar proportions.

Pycnodus vasseuri Savornin
Fig. 21g

1915 *Pycnodus vasseuri* Savornin: 376; fig. 5. Ypresian, Tocqueville, Algeria.

The species is based on one splenial. The photograph in Savornin's paper is very indistinct but measurements given by Savornin show that this specimen differs in tooth proportions from *P. maliensis*. It appears to be similar to *P. toliapicus* and probably should be synonymized with it.

Pycnodus pellei Priem
Fig. 21e

1903 *Pycnodus pellei* Priem: 402; pl. 13, fig. 5. Lower Eocene, Gafsa, Tunisia.
1952 *Pycnodus pellei* Priem; Arambourg: 229; pl. 37, fig. 29. Lower Eocene, Kouif, Algeria.

This species is known only by two splenial dentitions. The average length/breadth index of the medial teeth of *P. pellei* falls just within the upper limit of that of *P. maliensis*. However, the first and second lateral teeth of *pellei* are so much narrower than those of *maliensis* that they are obviously distinct species. The splenials of *P. pellei* resemble Stromer's specimens St5 and M1 but as Stromer says the first lateral teeth are slightly narrower in *pellei*, the medial and second lateral teeth slightly wider and the teeth of *P. pellei* are larger (average width of medial teeth 22 mm) than St5 and M1. Considering the small number of specimens involved I cannot say whether these differences are significant enough to warrant separation of *P. pellei* splenials and St5 and M1 into different species.

Pycnodus mokattamensis Priem
Fig. 21f

1897 *Pycnodus mokattamensis* Priem: 217; pl. 7, fig. 11. Lowest Lutetian, Mokattam, Egypt.
1899 *Pycnodus mokattamensis* Priem; Priem: 241; pl. 2, fig. 1. Lowest Lutetian, Mokattam, Egypt.

Two incomplete splenials of this species have been described. The splenials differ from those of *P. maliensis* in all of the characters listed in the diagnosis (p. 5). The splenials also differ from *P. toliapicus* (and synonyms) and *P. pellei* in having relatively narrow medial teeth which are oval in shape. *P. mokattamensis* also has narrower subcircular first lateral teeth.

Pycnodus bowerbanki Egerton
Figs 22–24

1877 *Pycnodus bowerbanki* Egerton: 4; pl. 3, fig. 2. Ypresian, England.
1895 *Pycnodus bowerbanki* Egerton; Woodward: 279.
1966 *Pycnodus bowerbanki* Egerton; Casier: 106; pl. 11, fig. 6.

This is the largest (average width of medial teeth 25·5 mm) of the Tertiary *Pycnodus* species and was previously known by one splenial only (BMNH 38824, Fig. 23). It is similar to *P. toliapicus* except that the medial and first lateral teeth of BMNH 38824 are relatively wider. It resembles *P. maliensis* in the proportions of the medial and first lateral teeth. However, the second lateral teeth are subcircular and only just wider than long. Because of this and the overall larger size *bowerbanki* is considered a separate species.

The specimen labelled GAO 7 (Fig. 24) collected by Lavocat from Mali, two almost complete splenials BMNH P.60916–7 (Fig. 22) and several fragments showing one or two tooth rows collected during the 1981 expedition differ significantly from the other Mali splenials. These specimens have larger teeth (average width of medial teeth 21·7 mm) than *P. maliensis* specimens and the medial teeth are not bevelled at the outer end. The first laterals are rectangular and twice as wide as long. The major difference from *maliensis* is that the present specimens have subcircular rather than elliptical second lateral teeth. The tooth proportions of these specimens are extremely similar to those of *P. bowerbanki* and they are therefore identified as *P.* cf. *bowerbanki*. All of these larger specimens collected on the 1981 expedition come from the oolitic deposit. Most were collected at Tamaguélelt but one specimen (BMNH P.60917) is from the oolitic deposit at the Samit locality.

Madden (1982) reports pycnodont teeth from the Umm Himar Formation, Saudi Arabia. He describes three medial teeth and one first lateral tooth from a large *Pycnodus* species. Madden's specimens are slightly larger than medial teeth of *bowerbanki* and represent the largest Tertiary *Pycnodus* known. The proportions of the medial teeth from Saudi Arabia are very similar to those of *bowerbanki*. No complete specimens have been found in the Umm Himar Formation and without second lateral teeth it is not possible to identify this large *Pycnodus* species. However, the Mali specimens show that large *Pycnodus* specimens, very similar to *bowerbanki*, do occur in Africa and it is possible that Madden's large *Pycnodus* sp. teeth are the same as the Mali ones and *P. bowerbanki*.

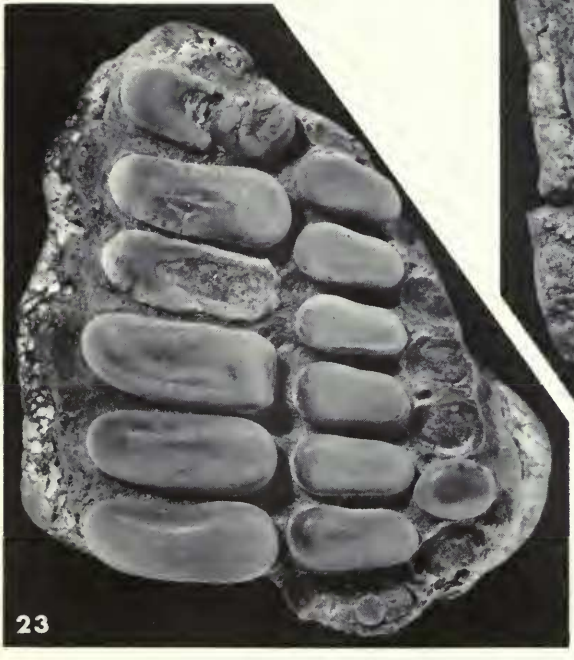
Vomers

The species where vomerine dentitions are known are reappraised and compared with each other and with *P. zeaformis* and *P. jonesae*. The length as a percentage of the breadth of vomerine teeth of Tertiary *Pycnodus* species is given in Table 2.

Pycnodus variabilis Stromer
Figs 25a–c, 27

1905 *Pycnodus variabilis* Stromer: 191; pl. 16, figs 33, 34. Lowest Middle Eocene, Mokattam, Egypt.

Stromer described two vomers under this name. They have narrow subtriangular median teeth with a very convex anterior border and a straight posterior border. The first lateral teeth are



Figs 22–24 Splenials of *P. bowerbanki*, all ×1. Fig. 22, BMNH P.60917. Fig. 23, holotype BMNH 38824. Fig. 24, GAO 7.

small and not much wider than long. They alternate with the median teeth and are shaped like an asymmetrical triangle with the greatest height nearer the midline of the vomer. In this respect they differ from other Tertiary species. The second lateral teeth are subtriangular to oval and have their longest axes at 60°–90° to those of the median teeth. The outer edges of the second lateral teeth are often worn and this accentuates their anteroposterior length. This is the shape and orientation of second lateral teeth found most in *Pycnodus* vomers. *P. variabilis* vomers therefore differ from *P. zeaformis* in all characters mentioned in the diagnosis (p. 7), and from

Table 2 Relative measurements[2] of teeth of vomers of Tertiary *Pycnodus* species. (A) Length as a percentage of width of teeth, average of each tooth row with ranges given in brackets and number of specimens measured. (B) Average width of teeth in mm, all teeth in each row measured.

	A				B	
	median	first lateral	second lateral	number of specimens measured	median	first lateral
P. zeaformis	40·7 (36–49)	45·8 (39–51)	52·9 (42–68)	15	11·0	7·5
P. jonesae	44·6 (39–52)	65·0 (56–78)	71·1 (64–86)	6	8·9	5·4
P. variabilis	70 (69–71)	88 (75–101)	163	2	5·6	4·1
P. praecursor	65·8	113	125	1	5·6	4·5
TGE 625	69·7	96·9	156	1	4·6	3·4
P. tattami	62·2	70·4	110	1	12·6	8·8
P. thamallulensis	60·6	85	—	1	15	10
P. mokattamensis	71·9	75	137	1	14	12
P. munieri	63·3	81·2	154	1	11	8
P.60635	55·9	72	157	1	6·7	4·5
P.10121	65	77	148	1	11·7	8·3
P. lemellefensis	54	66·6	100	1	18	12
P. legrandi	60·6	66·6	125	1	16	12
P. savini	51·1	75	122	1	22	12
P. pachyrhinus	62 (60–64)	73 (72–74)	138·5 (130–147)	2	11·8	8·8

[2]A copy of the full measurements of type material of *P. zeaformis* and *P. jonesae* is deposited in the Palaeontology Library of the British Museum (Natural History).

P. jonesae in the shape of the median teeth. The vomers were identified as *P. variabilis* by Stromer because of their association with splenials he described as *variabilis*. The vomers differ from previously described species in the shape of the median and first lateral teeth and so there is no reason to reassign the vomers, unlike the splenials where it is suggested (p. 12) that all but St2 (Stromer 1905: pl. 16, fig. 36) be reassigned.

In the Mali fauna the smallest vomer, TGE 625 (average width of median teeth 4·8 mm) (Figs 25c, 27), is very different from the others. It is identified as *P. variabilis* because it has narrow subtriangular median teeth, triangular first lateral teeth with their apices nearer the midline, and oval second lateral teeth orientated at 70°–90° to the median teeth.

Pycnodus praecursor Dartevelle & Casier
Fig. 25d

1949 *Pycnodus praecursor* Dartevelle & Casier: 212; pl. 17, figs 7a, b. Palaeocene, Landana, Cabinda, Angola.

The vomers figured by Dartevelle & Casier resemble the vomers of *P. variabilis*. They have triangular median and first lateral teeth and oval second lateral teeth. These vomers therefore

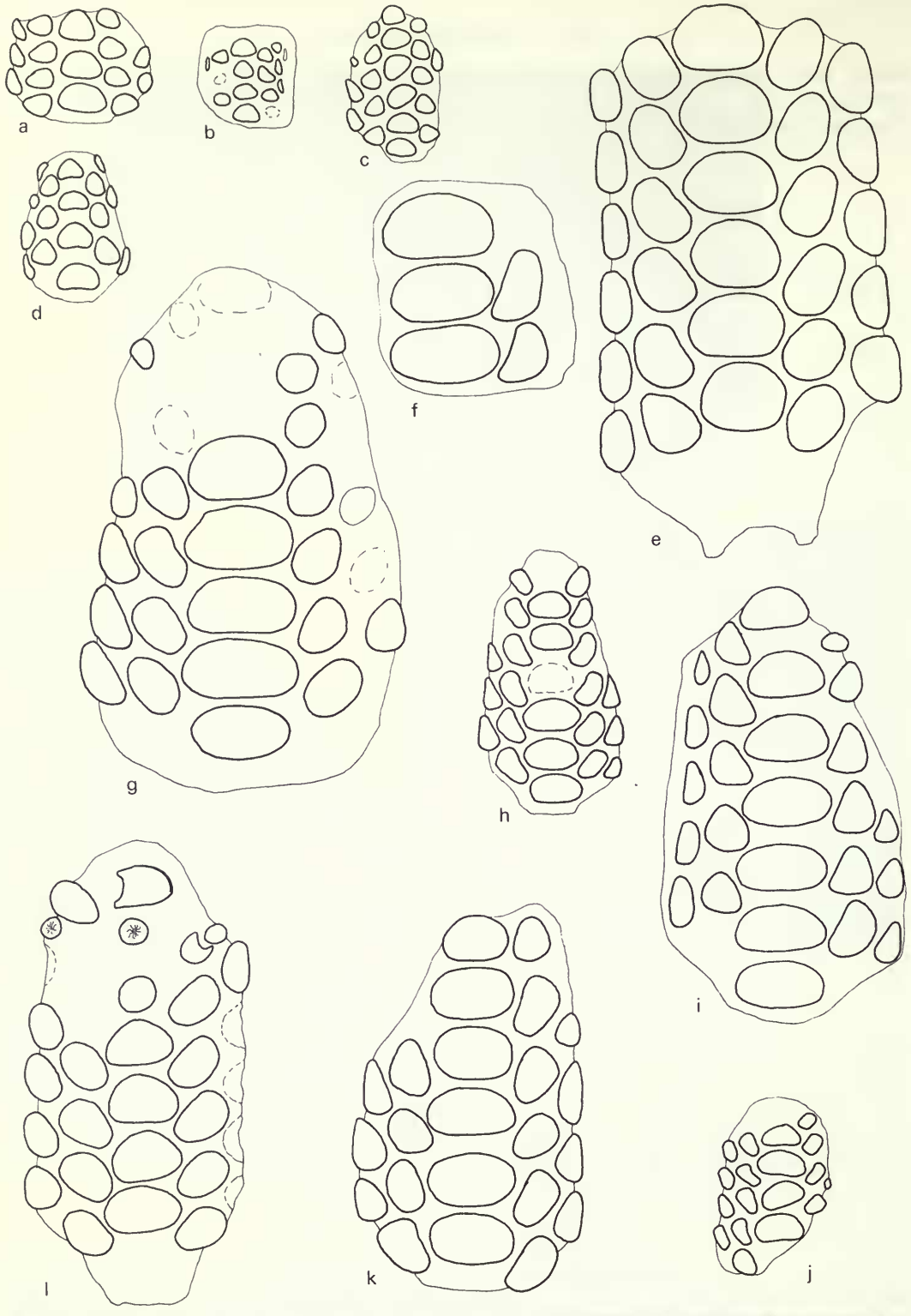


Fig. 25 Outline drawings of vomers of *Pycnodus* species to show differences in tooth shapes. All ×1, drawn from original photographs or drawings. The first and second lateral row teeth are slightly foreshortened. a, *P. variabilis*, specimen St. b, *P. variabilis*, specimen M. c, *P. variabilis*, TGE 625. d, *P. praecursor*. e, *P. mokattamensis*, holotype. f, *P. legrandi*, holotype. g, *P. lemellefensis*, holotype. h, *P. munieri*. i, *P. munieri*, holotype. j, *P. munieri*, BMNH P.60635. k, *P. toliapicus*, BMNH P.10121. l, *P. pachyrhinus*, holotype BMNH P.610.

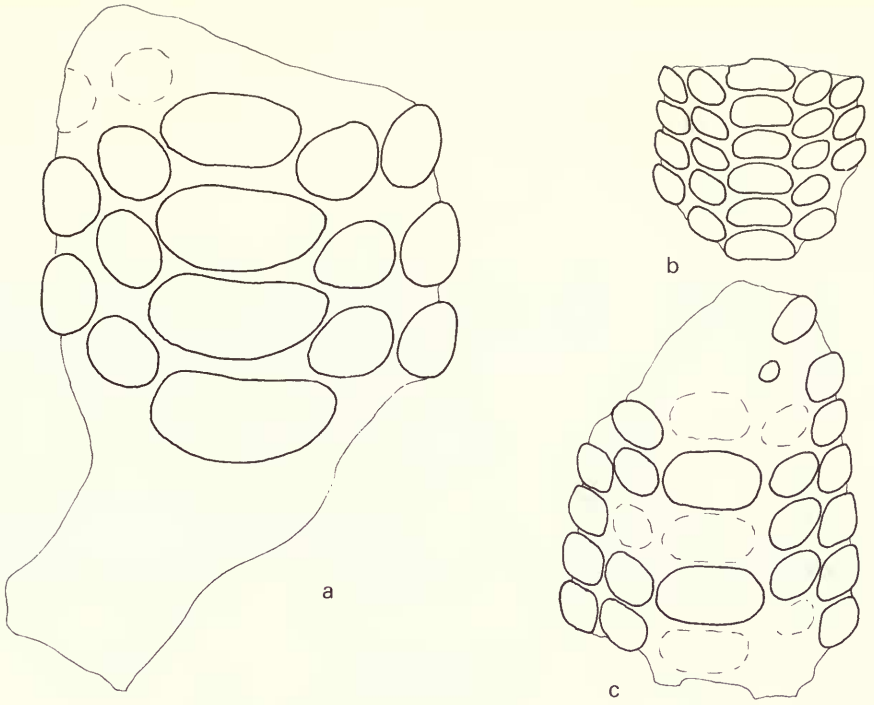


Fig. 26 Outline drawings of vomers of *Pycnodus* species, continued from Fig. 25. All ×1, drawn from original photographs or drawings. a, *P. savini*, holotype. b, *P. jonesae*, MLM 21. c, *P. tattami*, holotype BMNH P.18825.

differ from *P. zeaformis* and *P. jonesae*. Dartevelle & Casier say that the vomers resemble those of *P. tattami* in the width and open spacing of the median teeth. However, the median teeth of *P. tattami* are rectangular and the first lateral teeth are oval and not like those of *P. praecursor*. *P. praecursor* vomers should therefore be synonymized with *P. variabilis* vomers under the latter name.

Pycnodus tattami White
Fig. 26c

1935 *Pycnodus tattami* White: 42; figs 10,11. Landenian, Wurno, Nigeria.

The species is based on two specimens. The holotype (BMNH P.18825) is a medium-sized vomer (average width of median teeth 12 mm) differing from *P. zeaformis* in all characters mentioned in the diagnosis (p. 7). The proportions of the teeth in *P. tattami* are similar to those of *variabilis* but the tooth shape is different. The median teeth in *tattami* are rectangular and relatively slightly wider than those of *variabilis*. The first laterals are ovoid and are orientated at about 30° to the median teeth. The second lateral teeth differ from those of all other species in being square or lozenge-shaped with their longest axes at about 45° to those of the median teeth. The second specimen described by White (BMNH P.18826) is much smaller than the holotype and White suggested that it was a juvenile and that the differences between the two are due to growth. The similarities he used to unite the two are the proportions of the teeth and the alignment rather than alternation of the first lateral and median teeth. White thought this arrangement was not found in any other Eocene species. This character is found in *P. zeaformis* but both specimens of *P. tattami* differ from *P. zeaformis* in other respects. The smaller

specimen of *P. tattami* does not seem to be assignable to any other Tertiary species, and I leave it as *P. tattami* despite the differences from the holotype.

Pycnodus mokattamensis Priem
Fig. 25e

1897 *Pycnodus mokattamensis* Priem: 217; pl. 7, figs 9, 10. Lower Lutetian, Mokattam, Egypt.
1915 *Pycnodus mokattamensis* Priem; Savornin: 371; fig. 1. Ypresian, Rilassa, Algeria.
1922 *Pycnodus mokattamensis* Priem; Leriche: 208; pl. 4, fig. 6. Lower Lutetian, Mokattam, Egypt.

Three vomers of *P. mokattamensis* have been described. All three resemble *P. variabilis* in having median teeth with arched anterior borders. However, the first lateral teeth of *mokattamensis* are oval to subtriangular and wider at the posterior end. Some of the first lateral teeth also have a slightly concave inner anterior border. The second lateral teeth are oval and have the longest axes at 90° to those of the median teeth. Most of the teeth have a central depression and crenulations around the edges, the characters used by Priem to distinguish *mokattamensis* from other species and to link the vomers with the splenials of *mokattamensis*. The vomers of this species are closest in appearance to *P. pachyrhinus* Egerton but as Priem points out the median teeth of *P. pachyrhinus* have even more arched anterior borders. The first lateral teeth in *pachyrhinus* are oval but are slightly wider at the anterior end, not the posterior end. The vomers of *mokattamensis* differ from *P. zeaformis* and *P. jonesae* in all the characters listed in the diagnoses of the latter two species.

Pycnodus munieri Priem
Figs 25h–j, 28

1902 *Pycnodus munieri* Priem: 44; fig. 1. Eocene, Couiza (Aude), France.
1908 *Pycnodus munieri* Priem; Leriche: 7; pl. 1, fig. 4. Ypresian, Fabrezan (Aude), France.

This species is known by two fairly complete vomers, the one figured by Leriche being described as juvenile. The vomers have ovoid median teeth, slightly arched in front and with a straight posterior border. The first lateral teeth are subtriangular with a wider posterior end and have a concave inner anterior border. The inner corners of the first lateral teeth tend to extend inwards between the median teeth. The second lateral teeth are oval and aligned with the first lateral teeth in Leriche's specimen. In Priem's specimen, however, the second lateral teeth are aligned with the first lateral teeth on one side but alternate with them on the other, showing that this character can vary in an individual as well as within a species. In the Mali fauna two specimens, BMNH P.60635 (Figs 25j, 28) and P.60922, are identified as *P. munieri*. They especially resemble the specimen figured by Leriche (Fig. 25h) and have all the characters described for *P. munieri*.

P. munieri differs from *P. variabilis* and *P. pachyrhinus* in the shape of the first lateral teeth and in having more oval median teeth. The first lateral teeth of *P. pachyrhinus* are wider at the anterior end, not the posterior end as in *P. munieri*. *P. munieri* differs from *P. mokattamensis* in having slightly wider median teeth and no crenulations around the teeth. *P. munieri* differs from *P. zeaformis* and *P. jonesae* in all characters mentioned in the diagnoses (p. 7).

Pycnodus lemellefensis Savornin
Fig. 25g

1915 *Pycnodus lemellefensis* Savornin: 371; fig. 2. Lower Eocene, Bordj-Redir, Algeria.

The species is represented by one medium-sized vomer (average width of median teeth 18 mm). The median teeth are ovoid and relatively wider than those of *mokattamensis* and *variabilis*. Savornin said that his specimen differed from other Tertiary species in having second lateral teeth aligned with the first lateral teeth and not alternating with them. As noted above, both states of this character occur in one individual of *P. munieri*. Savornin's other main reason for erecting his new species is that the median teeth have a notch in the anterior outer edge. However, from his figure this character occurs on one side only on two out of five

median teeth. It is a character common in pycnodont dentitions that where two teeth grow closely together their shape may be altered. In all respects the vomer resembles those of *P. munieri* and should be synonomized with it. It differs from *P. zeaformis* and *P. jonesae* in all characters listed in the diagnoses of those species.

Pycnodus legrandi Savornin
Fig. 25f

1915 *Pycnodus legrandi* Savornin: 374; fig. 3. Lower Eocene, Tocqueville, Algeria.

An incomplete vomer is the only specimen of this species. Savornin differentiated it from *lemellefensis* because the tooth-bearing surface of the vomer of *legrandi* is biangular when viewed from behind, and not regularly arched. This character, however, is variable within the Mali species, and can be affected by wear. The vomer is otherwise very similar to those of *lemellefensis* and *munieri* and *P. legrandi* should be synonymized with *P. munieri*.

Pycnodus thamallulensis Savornin

1915 *Pycnodus thamallulensis* Savornin: 375; fig. 4. Lower Eocene, Tocqueville, Algeria.

This species is known by one very incomplete vomer. The median tooth is rectangular and so differs from those of Savornin's other specimens in having a less arched anterior border. The first lateral teeth, of which only two are preserved, are regularly oval and have their longest axes at 45° to that of the median tooth. Savornin compares this specimen to *P. munieri* and notes a similarity except that the first lateral teeth are oval and there is a large space (5 mm) between the median and first lateral rows. In these respects the specimen closely resembles *P. tattami* White.

Pycnodus savini Priem
Fig. 26a

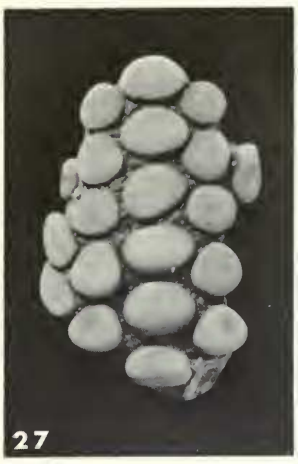
1902 *Pycnodus savini* Priem: 46; fig. 2. Middle Eocene, Villespy (Aude), France.

Priem described this species from Aude on an incomplete vomer of larger size (average width of median teeth 22 mm) than *P. munieri* (average width of median teeth 11 mm). The specimen differs from all other Tertiary species in having oval median teeth with slightly pointed outer ends. The median teeth also tend to have a slightly concave anterior border and a convex posterior one. The median teeth are unlike those of other species except *P. zeaformis* and *P. jonesae* in that they are about twice as wide as long. However, the teeth of the first and second lateral rows are oval and orientated respectively at about 60° and 90° to the median teeth. In these respects *P. savini* differs from *P. zeaformis*. It differs from *P. jonesae* in the shape of the median teeth. Priem's view that this specimen represents a distinct species seems justified.

Pycnodus pachyrhinus Egerton
Figs 25l, 29

1877 *Pycnodus pachyrhinus* Egerton: 54; pl. 4, figs 1, 2. Ypresian, Kent, England.
1895 *Pycnodus pachyrhinus* Egerton; Woodward: 278. Ypresian, Kent, England.

The species is based on an almost complete vomer, BMNH P.610. The specimen resembles *P. mokattamensis* in having median teeth with strongly arched anterior borders and straight posterior ones. The first lateral teeth are oval but slightly wider at the anterior end. The second lateral teeth are also oval when unworn. In these respects it differs from *mokattamensis* and *munieri*. Woodward identified a worn vomer, BMNH P.170, as *P. pachyrhinus*. This specimen is similar to the holotype but has more oval median teeth. However, the first lateral teeth are so similar to those of the holotype that BMNH P.170 is probably correctly identified as *P. pachyrhinus*. *P. pachyrhinus* differs from *P. zeaformis* and *P. jonesae* in all characters mentioned in the diagnoses. As Egerton said, there is no evidence to indicate whether *P. pachyrhinus* is a vomer of *P. toliapicus* or of *P. bowerbanki*, both of which are also found in



Figs 27–29 Vomers of *Pycnodus* species. Fig. 27, *P. variabilis*, TGE 625, ×2. Fig. 28, *P. munieri*, BMNH P.60635, ×2. Fig. 29, *P. pachyrhinus*, holotype BMNH P.610, ×1.

the London Clay, or of some other species, therefore the name *pachyrhinus* should remain valid.

Pycnodus toliapicus Agassiz
Fig. 25k

1966 *Pycnodus toliapicus* Agassiz; Casier: 104; pl. 11, fig. 5. Red Crag (London Clay derived), Suffolk, England.

Casier described a vomer, BMNH P.10121, as *P. toliapicus*. He stated that it is similar to BMNH P.170 and BMNH P.610 (both *P. pachyrhinus*) and suggested that *P. pachyrhinus* should be synonymized with *P. toliapicus*. The proportions of the teeth of BMNH P.10121 and *P. pachyrhinus* are similar but the tooth shape is very different. BMNH P.10121 resembles *P. munieri* much more closely than it does *P. pachyrhinus* in that the median teeth in BMNH P.10121 are more or less ovoid, and the first lateral teeth trapezoidal with a wider posterior end and a concave inner anterior border in some teeth. BMNH P.10121 is probably a specimen of *P. munieri*; hence *P. toliapicus* would still be known only by splenial dentitions.

Two other *Pycnodus* species are known from the Tertiary, *Pycnodus apodus* (Volta) (= *P. platessus* Agassiz), and *Pycnodus gibbus* Agassiz. These are based on complete fishes from the Middle Eocene of Monte Bolca, Italy. In these species the dentitions are extremely small. There are few teeth in each row and these decrease rapidly in size anteriorly so that the anterior teeth in all rows are barely wider than long. The posterior teeth in the splenials are oval in the medial and first lateral rows but circular in the second lateral row. The vomerine teeth are poorly known but are also very small and decrease rapidly in size forwards. I do not believe any other described species is synonymous with either of these two species, because of the small size of the dentitions and the narrowness of the second lateral teeth on the splenials.

Conclusion

The above survey leads me to suggest that the number of Tertiary *Pycnodus* species known only by splenials or vomers should be reduced.

The following species should be considered valid.

Pycnodus bowerbanki Egerton, splenials
Pycnodus jonesae sp. nov., vomers.
Pycnodus maliensis sp. nov., splenials
Pycnodus mokattamensis Priem, splenials and vomers
Pycnodus munieri Priem, vomers. This species to include *P. lemellefensis* Savornin, *P. legrandi* Savornin and Casier's (1966) *P. toliapicus* specimen, BMNH P.10121.
Pycnodus pachyrhinus Egerton, vomers
Pycnodus pellei Priem, splenials
Pycnodus savini Priem, vomer
Pycnodus tattami White, vomers
Pycnodus thamallulensis Savornin, vomer. This species may be the same as *P. tattami.*
Pycnodus toliapicus Agassiz, splenials. This species to include *Periodus koenigii* Agassiz, Stromer's (1905) specimens St5 and M1, *P. variabilis* var. *togoensis* Stromer, *P. vasseuri* Savornin, and *P. praecursor* Dartevelle & Casier, splenials only.
Pycnodus variabilis Stromer, vomers and splenials. This species to include Stromer's (1905) specimen St2, White's (1935) specimen BMNH P.18826, and *P. praecursor* Dartevelle & Casier, vomers only.
Pycnodus zeaformis sp. nov., vomers.

The abundant *Pycnodus* material from Mali has proved useful in showing the variation that can occur within a species, so clarifying the features that can best be used for diagnosis. Tooth shape can vary within *Pycnodus* species, and single teeth or very incomplete vomers or splenials cannot be identified with any certainty. The relative proportions of the teeth in the various rows can be a useful diagnostic feature but this must be combined with overall tooth shape, especially in the vomers.

Table 3 shows the stratigraphical range of the Tertiary *Pycnodus* species discussed previously. Although the pycnodonts are common in the phosphate deposits in Mali they are not useful for dating purposes. Three species found in Mali (*P. variabilis, P. munieri* and *P. bowerbanki*) are known elsewhere from the Landenian to the Lutetian. This is the range of ages that has also been suggested for the Mali phosphates (Lowest Eocene by R. T. Moody and Middle Eocene by H. Radier, see Introduction), so the range of these *Pycnodus* species does not help to resolve the problem of the age of the Mali phosphates.

The Mali specimens do illuminate the problem of tooth replacement in pycnodonts. In these specimens the main difference between large and small dentitions of the same species is that the anterior region of the large dentitions is covered in small round irregularly-arranged teeth instead of the normal elliptical teeth arranged in rows. According to Thurmond (1974: 110) and Woodward (1895: 194) pycnodont dentitions grew by the addition of new and larger teeth at the posterior end of the vomer and splenial. The anterior teeth were worn until they were no longer functional and then lost (whether they were shed or resorbed is not stated). Thurmond and Woodward also said that there does not appear to be any replacement of individual teeth. This would mean that the anterior teeth are the oldest, and therefore the small, round, anterior teeth in the large Mali dentitions would be those that had been functional in the juvenile and should show most wear. Woodward (1893: 433) believed that juveniles would have had small round teeth. However, as stated above the small specimens from Mali have the characteristic regularly-arranged elliptical or oval teeth and very few small round teeth. In the larger dentitions the most anterior normal-shaped teeth show more wear than the posterior ones but the small round teeth in front of them show little or no wear. In many large specimens the most anterior elliptical teeth are so worn that the pulp cavity is exposed. In some, part of the tooth has disappeared entirely (apparently by resorption rather than wear) and small round teeth can be

Table 3 Stratigraphical distribution of Tertiary *Pycnodus* species.

	PALAEOCENE		LOWER EOCENE	MIDDLE EOCENE
	Montian	Landenian	Ypresian	Lutetian
P. variabilis				+
P. v. var. *togoensis*		+		
P. vasseuri			+	
P. praecursor	+	?	+	
TGE 625			+ ?	+
P. pellei			+	
P. mokattamensis				+
P. pachyrhinus			+	
P. tattami		+		
P. thamallulensis			+	
P. munieri			+	
BMNH P.60635			+ ?	+
BMNH P.10121			+	
P. lemellefensis			+	
P. legrandi			+	
P. toliapicus			+	
P. koenigi			+	+
P. savini			+	
P. bowerbanki			+	
GAO 7			+ ?	+
BMNH P.60917			+ ?	+
P. maliensis			+ ?	+
P. zeaformis			+ ?	+
P. jonesae			+ ?	+

observed within the outline of the original ellipse (e.g. see tooth marked *a* in Fig. 13). No small teeth have been observed within the pulp cavity of intact teeth. Examination of numerous large and small vomers and splenials from Mali gives the impression that the dentitions grew by the addition at the rear of new, larger elliptical teeth but also that the juvenile pattern of regular elliptical teeth was progressively replaced from the front by irregularly-arranged small round teeth. This replacement was not direct as a phyllodonts (Estes 1969) but appears to have been interstitial with resorption of part of the pre-existing worn tooth. Sections of dentitions of *Pycnodus* and other pycnodont genera have not yet shown tooth replacement conclusively, but future work involving sectioning and possibly X-raying of the Mali specimens may do so. The phenomenon of small round irregularly-arranged teeth is common in *Pycnodus* species but rare in other pycnodont genera. However, I have observed it in vomers and splenials of the genera *Gyrodus, Coelodus, Eomesodon* and *Macromesodon*. The whole question of tooth replacement in pycnodonts merits further study.

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